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NEW GENERA AND SPECIES OF BRANCHIOBDELLID WORMS (ANNELIDA: CLITELLATA)

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In the taxonomic study of any group of animals, the discovery of possibly primitive survivors of ancestral stocks commands attention. The new genera and species of branchiobdellid worms described herein are such animals. This paper treats of them as a necessary prelude to further considerations of evolution within the order Branchiobdellida.

In addition to the financial support of the National Science Foundation (grant GB–372) and release from academic duties afforded by a Visiting Research Associateship at the Museum of Natural History, Smithsonian Institution, I should like to acknowledge the help given me by Drs. Alejandro Villalobos Fiqueroa and James J. Friauf, Jr., who collected specimens of three of the species described in this paper. Mrs. Virgie F. Holt helped collect specimens of the other species and with the preparation of the manuscript. Dr. Villalobos and Dr. Horton H. Hobbs, Jr., very kindly identified the host crayfish. Dr. Hobbs, as for nearly all of my writings, has given generously of his time in a critical reading of the manuscript.

The methods and terminology used in the taxonomic study of the branchiobdellids have been described before (*inter alia*, Holt, 1953, 1960a, pp. 57, 62–64; 1968; Hoffman, 1963, pp. 277–292). Since, however, within what Stephenson, 1930, calls a homogeneous group of annelids, thirteen genera are now known and three new ones are erected in this paper,

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some attention to what constitutes a genus is necessary and appropriate.

In most species groups there is a distinctive generic facies, illustrated by such genera as *Ceratodrilus* Hall, 1914, and *Xironogiton* Ellis, 1919, produced by features of body form and ornamentation. Yet, some characters, presumably the result of convergent evolution, appear among some species of two or more genera otherwise considered distinct. An example is the presence of dorsal projections among species of *Ceratodrilus* and *Pterodrilus* Moore, 1895a. Such characters as this and others (raised dorsal ridges on the prosomites of trunk segments, peristomial lobes and tentacles, a flattened trunk, etc.) are too inconsistently correlated with features of the reproductive systems to be used reliably in the recognition of supraspecific taxa. They are, however, along with the general shape and appearance of the jaws, responsible for the superficial resemblances among species of most genera. Some genera, separated by what has been thought to be fundamental differences in the reproductive systems, are indistinguishable in external appearance, for instance, species of *Ankyrodrilus* Holt, 1965, and *Xironodrilus* Ellis, 1918 (Holt, 1965, pp. 9–10). With exceptions dictated by previous usage of generic names and the distinctiveness of groups of species characterized by jaw shape, external ornamentation and coherence of geographical distribution, *e.g. Ceratodrilus* (Holt, 1960a, pp. 57–58) and *Pterodrilus* (Holt, 1968b), the genera of branchiobdellids are based upon what are considered basic differences in the reproductive systems. This approach allows the development of theories of phylogenetic relationships that cannot be derived from a classification based upon non-genital characters. The genera now known, defined by these characters, seem to represent separate lineages.

The important features of the female system are associated with the spermatheca. This organ is subject to considerable intraspecific variability accounted for, presumably, by differences in its degree of distension with spermatozoa. Furthermore, constant differences that occur, the presence or absence of ental processes and various types of glandular or muscular thickenings of the wall of the spermathecal bulb, are not

correlated invariably with differences in the male genitalia regarded as generic characters. Yet it seems to be true that a spermatheca other than one composed of a simple muscular ectal duct and thin-walled bulb is associated with primitive features of the male reproductive system.

The most significant generic characters, then, are thought to be those of the male genitalia. The importance of the differences between the eversible as opposed to a non-eversible penis was recognized early (Moore, 1895b, p. 498). The hazards associated with this distinction arise from the difficulty of being sure in preserved animals of the exact functioning of the bursal complex housing the penis. It is rare that specimens in collections are found with everted or protruded penes, and observations of copulation in living animals, at least for North American species, have not been reported. Further, there exist species in which the penis is intermediate in structure between those which are indubitably eversible and those which are clearly protrusible. Since, however, these differences of the bursa and penis can be associated with other features of the male system, they are of generic value.

Among other features of the male genitalia believed to be important is the place of entry of the vasa deferentia into the spermiducal gland. In one group of genera the deferent ducts enter the spermiducal gland directly at its ental end. In other genera the ducts enter the gland somewhere along its length; that is, there is a blindly ending ental projection of the gland beyond the region at which the vasa deferentia enter it.

Finally, the structure referred to as the prostate, a diverticulum of the spermiducal gland may or may not be present. If present, it may vary from a slight *prostatic protuberance* produced by a few apparently non-glandular cells enclosing a small cavity on the anterodorsal side of the spermiducal gland to a large, tubular, blindly-ending gland that opens in common with the spermiducal gland into the ejaculatory duct. The presence or absence of the prostate, the major differences in its degree of separation from the spermiducal gland, and its histological differentiation, or lack thereof, seem to be valid generic characters.

The permutations of a relatively few characters within a group of species that are collectively distinguished by a common pattern of the male genitalia may be numerous. The genus *Cambarincola* Ellis, 1912, for instance, with a distinctive male system that remains basically similar throughout the genus, contains more than thirty easily recognizable species (23 nominal species and several undescribed ones in my collections). On the other hand, the state of knowledge of the branchiobdellids and perhaps the pattern of evolution within the order is such that several genera are, as now known, monotypic or composed of only a few species. The branchiobdellids present relatively few characters suitable for taxonomic analysis and the decision as to what constitutes a genus among them admittedly involves elements of arbitrariness and subjectivity. The system that I am developing, of which this paper constitutes a part, is based upon theories of phylogeny that have been presented in preliminary form elsewhere (Holt, 1968a).

Sathodrilus new genus

Type-species: Sathodrilus carolinensis new species, here designated.

Diagnosis: Medium-sized branchiobdellid worms (known species 1.6 to 4.6 mm in length) with two pairs of testes; unpaired nephridiopore on dorsum of segment III; body terete, without peristomial tentacles or dorsal projections on trunk segments; spermiducal gland with vasa deferentia entering entally; prostate, if present, consisting of bulb-like prostatic protuberance on anterior or dorsal border of spermiducal gland; ejaculatory duct present; penis eversible, but attached by cytoplasmic strands to inner wall of penial sheath and without cuticular hooks; spermatheca with or without ental process.

Etymology: From Greek, *sathon,* one with a large penis, and *drilus,* a penis, by extension worm. Masculine.

Affinities: Among the branchiobdellids with eversible penes, rudimentary (or vestigial) prostates or none, vasa deferentia entering the ental end of the spermiducal gland and a common or unpaired anterior nephridiopore are *Sathodrilus, Ceratodrilus, Oedipodrilus* Holt, 1967a, *Magmatodrilus* Holt, 1967b, and a second new genus erected herein, *Tettodrilus.* Of these, *Sathodrilus* is most closely related to *Ceratodrilus* and is the unnamed relative of the latter mentioned previously (Holt, 1960a, p. 58). The two genera differ most strikingly in the presence of dorsal projections on segments II to VIII and the peristomial tentacles of *Ceratodrilus.* The jaws of the two genera are also quite different: those of *Sathodrilus* are subtriangular in shape, as is common among

other related genera (Figs. 2b, c, 3b, 4c, 6c, d), while those of *Ceratodrilus* are subrectangular with the tooth-bearing border slightly concave (Holt, 1960, Figs. 15–16).

Oedipodrilus has a distinct prostate, though it is incompletely divided from the spermiducal gland, and a completely eversible, tubelike penis that is unattached to the inner wall of the penial sheath portion of the bursa. In general, species of *Oedipodrilus* are smaller, more gracile animals than those of *Sathodrilus* and often have dorsal ridges on the prosomites of some or all body segments.

In *Magmatodrilus,* the vasa deferentia enter the large and very long spermiducal gland entally, but there is no prostate or prostatic protuberance. The most striking difference between these not too closely related genera is in the bursae. That of *Magmatodrilus* is exceptionally long, but the penial sheath is relatively very short. The penis, however, contrary to my former statement (Holt, 1967b, pp. 3, 4), is probably eversible, since it and the penial sheath have the structure of those of *Sathodrilus.* Most of the bursa of *Magmatodrilus* is composed of a thick muscular layer enclosing the atrial canal leading into the atrium proper. The jaws are entirely different in appearance from those of *Sathodrilus.* They are subrectangular with a 6/5 dental formula.

Sathodrilus is more distantly related to *Tettodrilus* (Figs. 9a, b, c, d). The prostate of *Tettodrilus* is incompletely divided from the spermiducal gland; that is, it does not extend to a common junction with the latter and the ejaculatory duct, but it is distinct with a well-defined prostatic bulb. In addition, the bursae and penes of the two genera differ markedly: the bursa of *Tettodrilus* is, in external appearance and shape, like that of the genus *Cambarincola,* but the penial sheath encloses an eversible penis that is different in structure from that of *Sathodrilus* (see below, p. 313).

The genera *Ellisodrilus* Holt, 1960b, *Cambarincola* and *Pterodrilus* have prostates, but mostly short, ovoid bursae, and all have protrusible penes. The other genera of the branchiobdellids lack prostatic protuberances or prostates, and, if the vasa deferentia enter the ental end of the spermiducal gland, the penis is protrusible.

Remarks: Species of *Sathodrilus* are described herein from localities in South Carolina, Georgia, and Mexico. The distribution may be more extensive than these records indicate, but species of the genus as defined are localized and rare; for although the branchiobdellid fauna of North America is comparatively poorly known, these are the only occurrences of *Sathodrilus* from over 1,600 locality records represented in my collections. This is the sort of distribution expected for a primitive group and *Sathodrilus* appears to stand close to the ancestral stocks of the genera *Cambarincola* and *Pterodrilus* and, in addition, to be closely related to the likewise localized species of *Ceratodrilus* and the possibly more advanced and certainly widespread, but still in some ways primitive, *Oedipodrilus.*

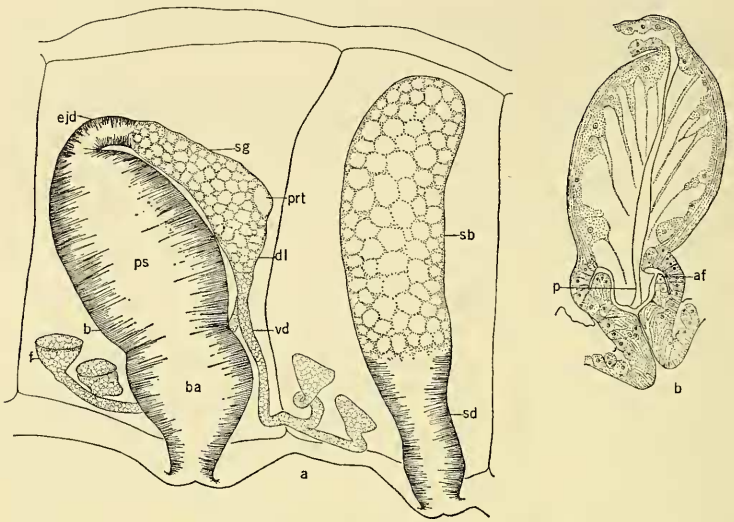

FIGURE 1. *Sathodrilus carolinensis: a,* lateral view of reproductive systems; *b,* longitudinal optical section of bursa and penis. Abbreviations: *b,* bursa; *ba,* bursal atrium; *dl,* deferent lobe; *ejd,* ejaculatory duct; *f,* male funnel; *af,* inner atrial fold; *p,* penis; *prt,* prostatic protuberance; *ps,* penial sheath; *sb,* spermathecal bulb; *sd,* spermathecal duct; *sg,* spermiducal gland; *vd,* vas deferens.

Sathodrilus carolinensis new species

Figures 1, 2

Type-specimens: Holotype, USNM 37107, one paratype, USNM 37108, and one paratype, PCH 1333, from *Cambarus latimanus* (LeConte) and *Cambarus* sp. taken in a small, sandy stream about 11.5 miles southwest of Anderson, Anderson County, South Carolina, on U. S. Highway 29, by Perry C. and Virgie F. Holt, 21 March, 1961.

Diagnosis: Slender, terete worms; upper lip entire, lower with shallow median indentation; no oral papillae; jaws small, delicate, dental formula 5/4; bursa large, about ¾ body diameter in length, bursal atrium about ⅓ total bursal length, penial sheath expanded, greater in diameter than bursal atrium; eversible penis attached by numerous thin strands to inner wall of penial sheath (Fig. 1b); ejaculatory duct short, less than ¼ length of bursa, thin-walled; spermiducal gland about twice its greatest diameter in length, tapering ectally from junction of ental-most and median thirds, with short, but distinct deferent lobes forming most of ental third of organ; prostatic protuberance at region of greatest diameter of spermiducal gland; spermatheca long, subequal to body diameter in length, clavate or spatulate, ectal duct widening gradually, spermathecal

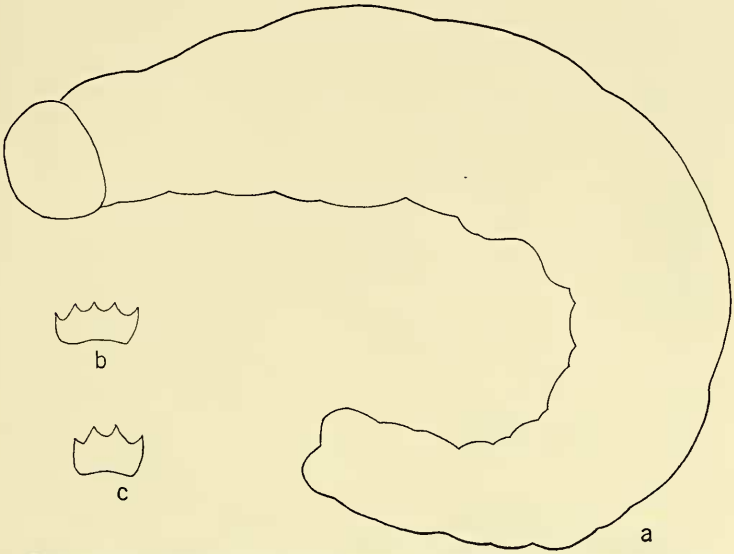

FIGURE 2. *Sathodrilus carolinensis: a,* holotype; *b,* upper jaw; *c,* lower jaw.

bulb not externally set off from ectal duct, thin-walled without ental process.

Etymology: The adjectival form of Carolina.

Description: Sathodrilus carolinensis is a medium-sized, slender worm. The three individuals of the type series have the following dimensions: *total length,* 3.1–4.1 mm; *greatest body diameter* (segment VIII), 0.39–0.57 mm; *head length,* 0.43–0.48 mm; *head diameter,* 0.27–0.30 mm; *diameter, segment* 1, 0.28–0.30 mm; *diameter, sucker,* 0.31–0.34 mm. The holotype is the longest of these specimens, but not consistently the greatest in other dimensions.

In external appearance (Fig. 2a), specimens of *S. carolinensis* are not remarkable. The head appears slender, although actually it is of rather usual proportions among the branchiobdellids. The peristomium, as usual, is divided by lateral indentations into dorsal and ventral lips. The upper lip is without lobes or projections; the lower is marked by a shallow, median indentation. Oral papillae are absent. Externally, the peristomium, again as usual, is set off by a shallow furrow; otherwise, there is one annular groove surrounding the head at about its midlength that is marked internally by what Ellis (1919, p. 243) called a "pharyngeal diverticulum" (actually an inner ring-like indentation of the wall of the pharynx) that I shall hereafter refer to as a *pharyngeal sulcus.* In some branchiobdellids there are more than one.

The jaws are small (Fig. 2b, c). The upper bears five sharply pointed

teeth, the lower four. Though not shown in the outline drawing, these teeth are separated by deep valleys in the body of the jaws that extend almost to their base (cf. Fig. 7d of the jaws of *Cronodrilus ogygius*).

The anterior nephridiopore is located as usual on the dorsum of segment III and is clearly visible in the holotype, but not in the other specimens.

A fairly well defined clitellum is present on segment VII. There are no supernumerary muscles in the prosomites of body segments, consequently the body outline is rather smooth.

The spermiducal gland is provided with well-marked, but relatively small, deferent lobes (Hoffman, 1963, pp. 286–287). These unite only a slight distance ental to the position of the prostatic protuberance. From the prostatic protuberance which marks the region of greatest diameter of the spermiducal gland, the latter narrows gradually so that its outer or ectal end as it joins the ejaculatory duct is no greater in diameter than the latter.

The prostatic protuberance is composed of a small group of cells that appear to have been evaginated by some force from the surrounding glandular epithelial cells. These cells of the prostatic protuberance are, however, much more finely granular than the cells of the epithelium of the spermiducal gland. There is a very small, but distinct space enclosed by the cells of the prostatic protuberance that is continuous by a very narrow canal with the lumen of the spermiducal gland. The prostatic protuberance is located on the anterior border of the spermiducal gland and is about ⅓ the length of the latter from its ental end (including the deferent lobes in the total length of the spermiducal gland), but median to and only slightly ectal to their junction.

The ejaculatory duct is short and thin-walled.

The bursa is marked (Fig. 1b) externally by a constriction between the penial sheath and atrial regions. The penial sheath, composing about ⅔ of the length of the organ, is somewhat greater in diameter than the atrial region of the bursa, but is quite thin-walled. The penis is clearly eversible: that of the holotype, indeed, is partially everted into the lumen of the bursal atrium. The penis is composed of a thin tubular membrane (Fig. 1b) apparently continuous with the inner cuticular lining of the bursal atrium and the cuticle of the outer body surface. This is attached by several thin strands to the inner wall of the penial sheath. The penial sheath is, as usual, covered by the peritoneum and its wall is composed of a layer of muscle the strands of which run lengthwise of the organ and continue as the muscular layer of the ejaculatory duct. These muscles are continuous with, and apparently are derived from, the outer circular muscles of the body wall. Internal to them, the penial sheath is lined with a layer of irregular cells with granular cytoplasm. Processes of these cells produce the strands that attach the inner wall of the everted penis to that of the penial sheath. In the uneverted position of the penis, most of the interior of the penial sheath portion of the bursa is composed of intercellular spaces.

The atrium of the bursa is enclosed by a relatively thick layer of muscle. A narrow canal leads from the outside into an expanded cavity which is the atrium proper. It is not clear that this portion of the atrium is eversible, but by analogy with specimens of *Oedipodrilus* with everted penes, it is not: the penis as it everts is simply exserted through the outer canal of the atrium. There is an inwardly projecting fold of the atrium, but it is not prominent (see below, p. 301).

The spermatheca is elongate club-shaped, extends to the dorsal wall of the coelom in segment V, and is in actuality, since it lies obliquely in the coelom and bends around and slightly over the gut, at least as long as the diameter of the segment. It gradually increases in diameter from the outlet pore almost to its ental end, and there is no external indication of the boundary between the spermathecal duct and the bulb. The spermathecal duct is relatively long and histologically similar to that described for other branchiobdellids (Holt, 1960a, p. 70) in which it is composed of muscle layers and lined with tall glandular cells, the inner ends of which project separately into the lumen. The bulb is thin-walled and has no features of note.

Variation: The three known specimens of *Sathodrilus carolinensis* differ in size and there are minor differences between them in proportions. From such a limited series, nothing else can be said about the variability of the species.

Affinities: The other new species of *Sathodrilus* described below are the closest known relatives of *S. carolinensis*. For a discussion of the affinities of all these species, see *S. veracruzicus* (p. 307, below).

Hosts: Cambarus latimanus (LeConte) and *C.* species.

Distribution: S. carolinensis is known only from the type-locality.

Material Examined: The type-series.

Sathodrilus villalobosi new species
Figure 3

Type-specimens: Holotype, USNM 37101, four paratypes, USNM 37102, and four paratypes, PCH 208, from *Paracambarus paradoxus* (Ortmann) taken at Tetela de Ocampo, Puebla, Mexico, by Alejandro Villalobos F., May, 1941.

Diagnosis: Medium-sized, terete branchiobdellids; upper lip entire, lower with shallow median indentation; no oral papillae; jaws heavy and dark, dental formula 1/4; bursa large, subequal to body diameter in length, bursal atrium less than ⅓ total bursal length, diameter of penial sheath less than that of bursal atrium; eversible penis composed of tube attached by few strands to inner wall of penial sheath; ejaculatory duct short, about ½ length of spermiducal gland; length of spermiducal gland about twice its diameter, about ⅓ that of the bursa, tapering toward each end from prostatic protuberance, and without deferent lobes; spermatheca with long, narrow spermathecal duct and globose bulb.

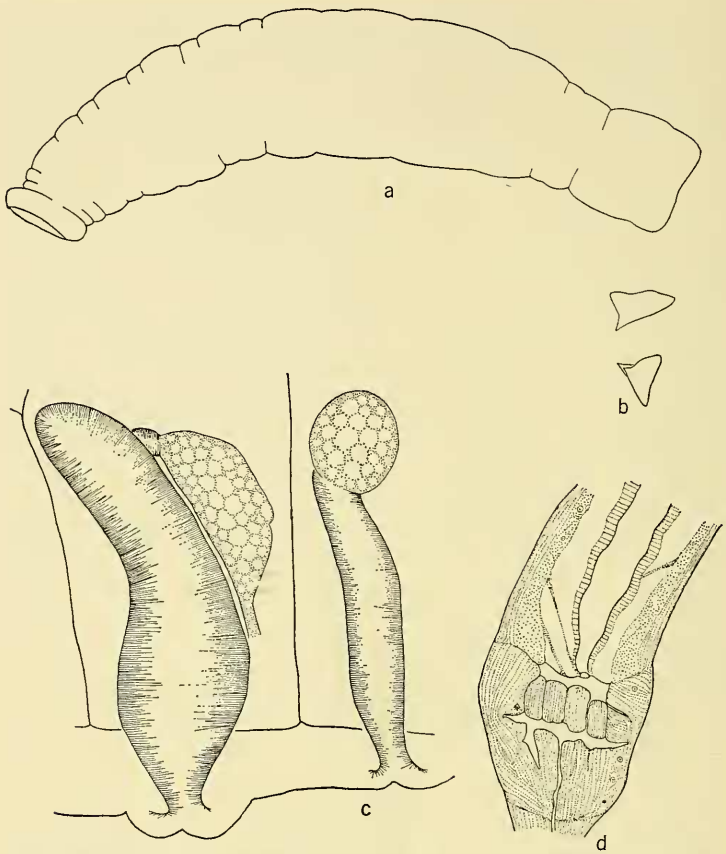

FIGURE 3. *Sathodrilus villalobosi: a,* holotype; *b,* lateral view of jaws, upper jaw above; *c,* lateral view of reproductive systems; *d,* longitudinal optical view of bursal atrium and ectal end of penis.

Etymology: I take pleasure in naming this Mexican species in honor of its discoverer, Dr. Alejandro Villalobos F. of the Universidad Nacional Autonoma de México, in appreciation of his hospitality and help in collecting branchiobdellids in Mexico.

Description: Sathodrilus villalobosi is a medium-sized worm. Five individuals of the type-series have the following dimensions: *total length,* 2.2–2.5 mm; *diameter, segment VI,* 0.42–0.49 mm; *head length,* 0.33–0.51 mm; *head diameter,* 0.34–0.45 mm; *diameter, segment I,* 0.32–0.39 mm; *diameter, sucker,* 0.32–0.39 mm.

The head is, in all specimens, short and thick, and though this appearance is exaggerated in the type series, it reflects the actual pro-

portions of the animals. Other than a similar proportionally greater thickness of the body segments, there is little worthy of comment about the external appearance of the animals. The upper lip is entire; the lower has a shallow median indentation. There are no oral papillae detectable in the type series, but each of a series of fifteen specimens collected later at Agua Fría show these papillae. The peristomium is set off by a deep encircling furrow. There is one other shallow groove surrounding the head and a single pharyngeal sulcus internally.

The jaws (Fig. 3b) are distinctive. They are larger and darker than those of S. *carolinensis*. The upper is triangular in both lateral and *en face* view and bears on its apex a large tooth. The sides of the upper jaw, which in most species with such jaws bear other teeth, are straight or slightly wavy and lateral teeth are represented by at most very low elevations. The lower jaw is triangular in lateral view and subrectangular in *en face* view. It bears two low rounded teeth on each side of the median line and two very low knobs lateral to these.

The anterior nephridiopore cannot be seen in the holotype, but a careful examination of other topotypical specimens shows it to be unpaired on the dorsum of segment III.

The body outline is smooth. The clitellum is not unusually prominent.

Deferent lobes are absent, or at least undetectable, and the vasa deferentia enter the narrow ental end of the spermiducal gland close together. The latter is small, about ⅓ of the length of the bursa and ½ its own length in diameter, narrowed at each end, and widest at the level of the prostatic protuberance.

The prostatic protuberance is located on the spermiducal gland about ⅓ the length from the ental end of the latter. It is composed of a small group of cells with a lumen between them that communicates with that of the spermiducal gland. The cells of the prostatic protuberance do not differ in appearance from those of the spermiducal gland.

The ejaculatory duct is short, about ½ the length of the spermiducal gland, and somewhat expanded. Its structure does not depart from that of other species.

The bursa (Figs. 3b, c) is large and subequal to the body diameter in length. The atrial region is somewhat shorter than ⅓ of the total length of the bursa. The diameter of the penial sheath is less than that of the atrial region and the penial sheath is not as expanded as that of S. *carolinensis* (cf. Fig. 1a).

The penis, an eversible tube, is longer than the penial sheath, looped and coiled entally within the cavity of the latter. A few strands attach it to the inner wall of the sheath, particularly at the ectal end. It is lined by a continuation of the cuticular lining of the bursal atrium and has an apparently muscular wall of some thickness (Fig. 3d).

Internally, the bursal atrium is characterized by a thick muscular fold that extends into the atrium and divides it into two compartments which communicate by the central space defined by the inner edge of the fold and narrow clefts extending from this space radially into the fold. This

feature of the bursa is not prominent in S. *carolinensis* (cf. Figs. 1b and 3d), and has been described for other species (Holt, 1949, pp. 544, 554, figs. 9, 16; Hoffman, 1963, p. 290, fig. 3). This atrial fold is itself eversible in these other species (ibid.); whether it is in S. *carolinensis* and S. *villalobosi* is unknown: it is not obvious that it is, but there is no doubt that the penis is eversible.

The spermatheca consists of a long spermathecal duct of the usual composition and a short, expanded, subglobose bulb set off by a constriction from the duct. There is no ental process.

Variation: Other than differences in size, differences in proportions that appear to be the effects of the method of killing and preservation and variations in the shape of the spermathecal bulb, and the prominence of the atrial fold depending upon the degree of expansion of the bursal atrium, there are no detectable variations in the material I have seen.

Affinities: See p. 307 below.

Hosts: *Sathodrilus villalobosi* is known from *Paracambarus paradoxus* (Ortmann) and *Procambarus contrerasi* (Creaser).

Distribution: In addition to the type-locality, *Sathodrilus villalobosi* has been taken from *Procambarus contrerasi* in Arroyo de San Diego, 3 km southeast of Agua Fría, Puebla, Mexico, by Alejandro Villalobos F., 23 October 1948, and by Alejandro Villalobos F., Patricio Gonzáles K., and Perry C. and Virgie F. Holt, 14 July 1962.

Material Examined: Other than the types listed above, 18 specimens from the type locality, PCH 208, two, PCH 202, and 15, PCH 1593, from Agua Fría, Puebla, in all, 35 specimens, have been studied.

Sathodrilus megadenus new species
Figures 4, 5

Type-specimens: Holotype, USNM 37109, two paratypes, USNM 37110, and two paratypes, PCH 1346, from *Cambarus latimanus* (LeConte) taken in a small stream, 3.1 miles north of Buchanan, Haralson County, Georgia, on U. S. Highway 27, by Perry C. and Virgie F. Holt, 25 March 1961.

Diagnosis: Stout, medium-large worms; lips entire or slightly lobed; no oral papillae; jaws of medium size, dental formula 5/4; bursa large, about ⅔ body diameter in length; length of bursal atrium about ⅓ total bursal length; penial sheath subglobose to pyriform, greater than bursal atrium in diameter; eversible penis attached by many strands to inner wall of penial sheath; ejaculatory duct long, subequal in length to penial sheath; spermiducal gland very long, length greater than body diameter, diameter about ⅐ its length, without deferent lobes; prostatic bulb present; spermatheca with spermathecal bursa and ental process, bulb cylindrical, of moderate size, total length about ¾–⅘ body diameter.

Etymology: From Greek, *mega*, large, and *adenos*, gland, in reference to the large size of the spermiducal gland.

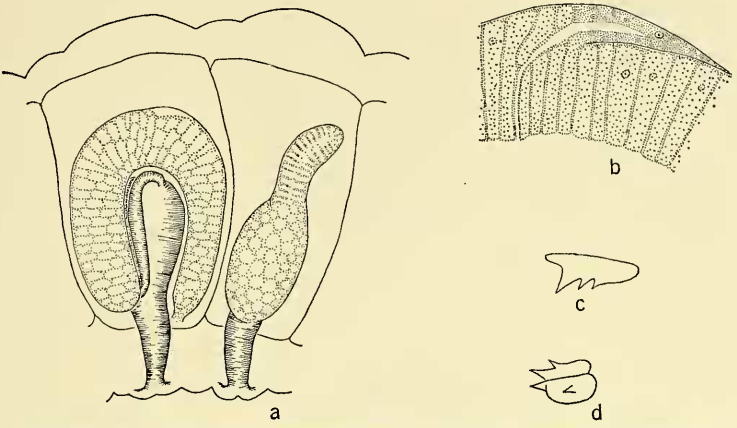

FIGURE 4. *Sathodrilus megadenus: a,* lateral view of reproductive systems; *b,* longitudinal optical section of prostatic protuberance and portion of spermiducal gland; *c,* lateral view of upper jaw; *d,* oblique view of lower jaw.

Description: Sathodrilus megadenus is a medium-large, stout worm. The five specimens of the type series have the following dimensions: *total length,* 3.9–4.6 mm; *greatest body diameter, segment VI,* 0.7–1.0 mm; *head length,* 0.8–1.0 mm; *head diameter,* 0.5–0.7 mm; *diameter, segment I,* 0.5–0.6 mm; *diameter, sucker,* 0.5–0.6 mm. The head is about ⅕ of the total length and almost as great in diameter. Segment VI, instead of the egg-bearing segment VII, has the greatest diameter. Segment I and the sucker are subequal to the head in diameter. Those dimensions confer a distinctive appearance within the genus upon individuals of *S. megadenus* (p. 297 and 300 above; Figs. 2a, 3a).

In other respects, the external appearance is not remarkable (Fig. 5). It is not possible in lateral view (and all the specimens are so mounted) to be sure that the lips are entire, but they appear to be so or at most only slightly lobed. The head shows little sign externally of segmentation: the peristomium is set off by a shallow encircling furrow and, at the region of the single pharyngeal sulcus, there is externally a still more obscure shallow furrow. The prosomites of at least the three anterior body segments are slightly raised. The clitellum is most prominent on segment VI instead of VII.

The anterior nephridiopore is unusually prominent in whole mounts for such large worms, but otherwise is unremarkable.

The jaws (Figs. 6c, d) are not unusual. The upper one is distinctly triangular in lateral and *en face* view with five sharply pointed teeth of which the median is the largest; the lower one is triangular in lateral view, subtriangular in *en face* view and bears four teeth, of which the paramedian ones are the largest.

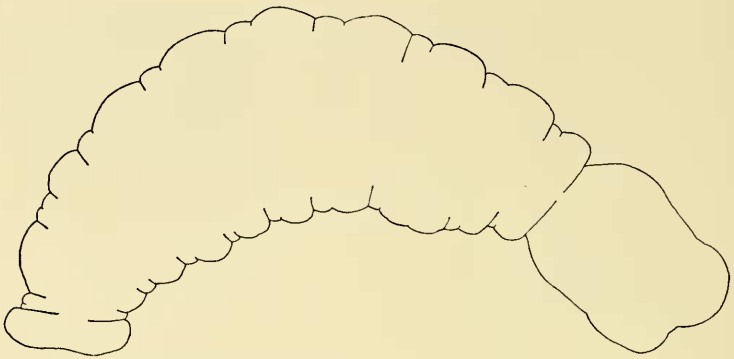

FIGURE 5. *Sathodrilus megadenus:* holotype.

The vasa deferentia enter the spermiducal gland directly; deferent lobes are absent. The large spermiducal gland, however, is the most striking character of the animal. It extends from the lower anterior border of the bursa posterodorsally over the bursa, ending at its junction with the ejaculatory duct opposite its beginning (Fig. 4a). The total length exceeds the greatest diameter of the body. It is also greater in diameter than those of related species. The diameter increases somewhat ectally, but not greatly, and it ends abruptly at its junction with the ejaculatory duct.

The prostatic protuberance is not easily seen in whole mounts, but it is present as a group of flattened epithelial cells enclosing a small lumen that communicates with that of the spermiducal gland (Fig. 4b) approximately at the midlength of the latter (Fig. 4a).

The ejaculatory duct is subequal in length to that of the penial sheath portion of the bursa and runs ventrad from the upper end of the latter along its posterolateral border (Fig. 4a). The epithelial lining and enclosing layer of muscle of the ejaculatory duct are prominent.

The bursa is quite large, though the greater diameter of segment VI makes it appear proportionally smaller than those of the other species of the genus. The penial sheath is subglobose, composes about ⅔ of the bursa, is thin-walled and much of its interior is occupied by spaces between the penis and the apparently muscular strands that attach the penis to its inner wall (cf. *S. carolinensis,* p. 298 and Fig. 1b).

The penis is difficult to interpret in my material. It appears to have a longitudinally folded cuticular lining and a thin investment of cytoplasm and to be somewhat longer, hence, slightly looped, than the enclosing penial sheath. There are numerous strands that converge from the inner wall of the penial sheath to attach to the penis. There is, however, no doubt as to its eversibility and essential similarity to those of other members of the genus.

The atrial region of the bursa widens somewhat abruptly from the outlet canal and its ental-most portion, the atrium proper, is enclosed by a thick layer of muscle. I cannot determine whether the atrial fold described above (p. 301) for *S. villalobosi* is present or not.

The spermatheca of *S. megadenus* is distinctive (Fig. 4a). There is a prominent sphincter formed of circular muscles around the outer portion of the spermathecal duct just ental to the spermathecal pore. The spermathecal duct is relatively narrow, but heavily muscular and its inner wall projects as a circular fold into a short, somewhat expanded, ental portion of the duct that is lined with a glandular epithelium typical of the lining of the spermathecal duct in other species. An everted "spermathecal bursa" (Holt, 1960a, p. 64) has never been seen, but the structure of the ectal part of the spermathecal duct of *S. megadenus* strongly suggests eversibility. The middle third of the spermatheca makes up the spermathecal bulb which is thin-walled and filled, as usual, with spermatozoa. The ental third is a narrow cylindrical process with a thick wall that almost obliterates its lumen. Apparently, the wall of this ental process is muscular, but this cannot be asserted with certainty in the absence of histological studies.

Variations: Other than minor differences in size, there are no detectable variations in my material.

Affinities: See p. 307 below.

Host: Cambarus latimanus (LeConte).

Distribution: Sathodrilus megadenus is known only from the type-locality.

Material Examined: The five specimens of the type-series.

Sathodrilus veracruzicus new species
Figure 6

Type-specimens: Holotype, USNM 37105, three paratypes, USNM 37106, and three paratypes, PCH 1623, from *Procambarus hoffmanni* (Villalobos), taken from Coyutla, Veracruz, by Alejandro Villalobos F., 16 April 1949.

Diagnosis: Small, slender, terete worms; lips entire; dental formula 5/4; bursa long, exceeding body diameter in length, penial sheath about ¾ total length, less in diameter than bursal atrium; eversible penis with thickened wall attached by few strands to penial sheath; ejaculatory duct short, about ⅓ length of spermiducal gland; spermiducal gland small, about ⅓ as long as bursa; no prostatic protuberance; spermatheca long, spermathecal duct subequal to body diameter in length, bulb cylindrical, long, no ental process.

Etymology: Of, or pertaining to, Veracruz.

Description: Sathodrilus veracruzicus is a small, slender, terete worm. Four specimens of the type series have the following dimensions: *total length,* 1.6–1.8 mm; *greatest diameter, segment VI,* 0.28–0.34 mm; *head length,* 0.26–0.29 mm; *head diameter,* 0.18–0.21 mm; *diameter, segment* 1, 0.19–22 mm; *diameter, sucker,* 0.20–0.22 mm.

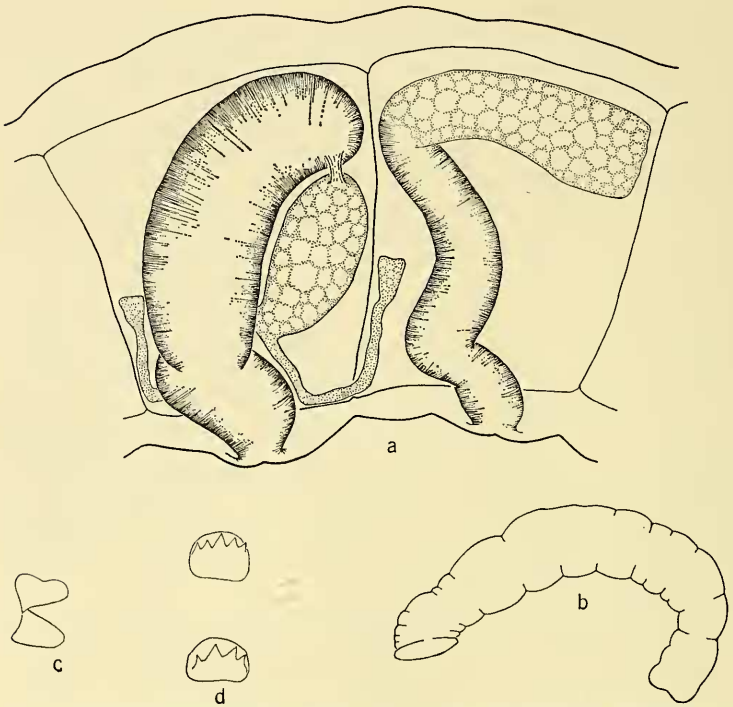

FIGURE 6. *Sathodrilus veracruzicus: a,* lateral view of reproductive systems; *b,* holotype; *c,* lateral view of jaws; *d, en face* view of jaws, upper jaw above.

The head of *S. veracruzicus* is not of unusual size or proportions. The lips are entire. The holotype appears to have at least some indistinct oral papillae, but these cannot be seen in other specimens. The external encircling furrow of the head is shallow and there is only one corresponding pharyngeal sulcus.

The jaws are of usual size for a small worm. The dental formula is 5/4; both jaws are triangular in lateral view, subrectangular in *en face* view (Fig. 6c, d).

The single nephridiopore occurs dorsally on segment III.

There are no dorsal ridges of the prosomites, but the intersegmental furrows are prominent. Clitellar glands are located upon the dorsa of segments VI and VII, but they are not prominent.

The vasa deferentia enter the spermiducal gland together at its ental end. There are no deferent lobes. The spermiducal gland is very small, about ⅓ the length of the bursa. The cells composing it are almost cuboidal (instead of the usual columnar type) and the lumen is dilated, perhaps a stage in a secretory cycle. The gland is only slightly tapered

at its ends and there is no sign at all of a prostate or prostatic protuberance.

The ejaculatory duct is short, but not as short as it appears to be in fore-shortened view (Fig. 6a). It is about ⅓ the length of the spermiducal gland.

Relatively, the bursa is very long, its length exceeding the body diameter. The penial sheath constitutes about ¾ of this length. The penis consists of a looped tube, with a wall of noticeable thickness, that is attached by a few strands to the inner wall of the penial sheath. The bursal atrium is expanded; its length is subequal to the diameter of the coelom in which it lies. Its wall is heavily muscular and folded, but it is not possible to determine clearly the inner structure of the atrium in the available specimens.

There is no spermathecal bursa. The spermathecal duct is long, subequal to the body diameter in length, with the usual glandular lining and muscle layers. The bulb is thin-walled, cylindrical and bent cephalad over the gut (Fig. 6a).

Variation: Except for differences in size and the possible presence of oral papillae in some specimens, no variations have been observed.

Affinities: Among the four species of *Sathodrilus* described herein, *S. carolinensis* and *S. villalobosi* are most closely related. *S. megadenus* and *S. veracruzicus* stand somewhat apart in different ways from the others.

S. veracruzicus is the smallest in body size, *S. megadenus* the largest, and the others lie in between, with *S. carolinensis* as a somewhat longer and more slender animal. Any phylogenetic significance that these differences in size and proportions may have is certainly obscure, but the smaller size and more slender proportions of *S. veracruzicus* are consonant with its other primitive features.

The jaws of all four species are similar in general shape and all, except *S. villalobosi,* have a 5/4 dental formula. Those of *S. veracruzicus* and *S. carolinensis* may more nearly approach the primitive conditions, but those of *S. megadenus* are not markedly different and the heavier jaws with a ¼ dental formula of *S. villalobosi,* apparently an advanced character, can easily have been derived from a common ancestor with jaws like those of *S. carolinensis* or *S. veracruzicus.*

Oral papillae are apparently present in *S. villalobosi* and *S. veracruzicus* and absent in the other species.

The spermiducal gland of *S. megadenus* is very different from those of the other species in its much greater absolute and relative size. That of *S. carolinensis* is the only one provided with deferent lobes, presumably a primitive feature, but that of *S. veracruzicus* lacks a prostatic protuberance, a still more primitive characteristic. *S. villalobosi* has a spermiducal gland with a prostatic protuberance and without deferent lobes. There are some minute but significant differences in the prostatic protuberances of the three species that have them. The cells composing the prostatic protuberance of *S. villalobosi* differ from those of the

spermiducal gland (as far as can be determined in whole mounts) only in being displaced to the outer surface of the gland; those of *S. carolinensis* appear more finely granular than the obviously secretory cells of the spermiducal gland; and, finally, those of *S. megadenus* form a distinctly flattened epithelium (Fig. 4b).

The ejaculatory ducts of all species are much alike. That of *S. megadenus* is unusual in its length, which is consonant with the unusual length of the spermiducal gland.

The bursa and its components unify the genus. In all the species the penial sheath region is large and encloses an eversible penis. The penial sheath of *S. villalobosi* is less in diameter than the atrial region; in the other species the reverse is true. The wall of the penis is thin, apparently composed only of cuticle with minute attachments of cytoplasmic strands, in *S. carolinensis*; in the other species it is thicker. The most striking bursal modification is found in *S. villalobosi* with its prominent inner atrial fold which is present, but not so greatly developed in *S. carolinensis*, and possibly is absent in the other species.

The spermatheca of *S. megadenus* has a spermathecal bursa and an ental process; the other species lack these structures and their spermatheca differ only in the shapes and relative sizes of the spermathecal ducts and bulbs. There does seem to be a relationship between such features of the spermatheca as those possessed by *S. megadenus* and large bursae with eversible penes and, on the basis of current views of phylogeny, they are primitive. In all the species of *Sathodrilus*, the spermathecal ducts are long and roughly correspond in length to the estimated length of the everted penes.

S. veracruzicus is the most primitive of these species, if it is admitted that the presence of a prostatic protuberance indicates an advance over its absence. *S. carolinensis* and *S. villalobosi* stand at about the same level of evolutionary advance and *S. megadenus* is the most specialized of the four. But such conclusions, although supported by the evidence, are not as important as the more general one that we have in these species a group of primitive forms that are the survivors of the stock that gave rise to the seven genera that collectively constitute the major portion of the North American branchiobdellid fauna.

Host: Procambarus hoffmanni (Villalobos).

Distribution: Known only from the type locality.

Material Examined: The type series.

Remarks: At one time, I considered *S. veracruzicus* a member of the genus *Oedipodrilus* and so stated in referring to the distribution of the latter (Holt, 1967a, p. 60). *Oedipodrilus* is composed of a number of species with collectively a wide geographical range that does not, however, to my knowledge, include Veracruz.

Cronodrilus new genus

Type-species: Cronodrilus ogygius new species, here designated.

Diagnosis: Branchiobdellid worms with two pairs of testes; unpaired

nephridiopore on dorsum of segment III; body terete, without peristomial tentacles or projections on trunk segments; spermiducal gland with vasa deferentia entering ectad to ental end; no prostate or prostatic protuberance; ejaculatory duct present; penis eversible, lying free in long, slender penial sheath; spermatheca with ental process.

Etymology: From Greek, *Kronos,* the father of Zeus, hence, an ancient ancestor, and *drilus,* a worm. Masculine.

Affinities: The North American genera of branchiobdellids with spermiducal glands that extend entally beyond the junction of the vasa deferentia with them are *Bdellodrilus* Moore, 1895b, *Ankyrodrilus* Holt, 1965, and *Xironogiton* Ellis, 1919. In addition, *Cirrodrilus* Pierantoni, 1905, from eastern Asia, and *Branchiobdella* Odier, 1823, of eastern Asia and Europe, have this arrangement of the vasa deferentia and the spermiducal gland. *Cronodrilus* differs from all these genera in the smaller size of its spermiducal gland and the shortness of the blindly-ending portion ental to the entry of the vasa deferentia. *Cronodrilus* and *Bdellodrilus* further differ in the structure of the jaws, those of *Bdellodrilus* are unusually modified (Moore, 1895b, fig. 9); in the numerous aggregations of glandular cells, including lateral and bursal ones, present in *Bdellodrilus* (Moore, 1895b, pp. 505–506, 522–523) and absent in *Cronodrilus*; in the branched spermatheca of *Bdellodrilus*; and in the generally thinner and more glandular body wall of *Bdellodrilus* which confers a distinctly parasitic appearance upon the genus. *Cronodrilus* and *Ankyrodrilus* differ in jaw structure. The jaws of *Ankyrodrilus* are more nearly rectangular and the teeth are differently arranged. The bursa and penis of *Ankyrodrilus* are unlike those of any other branchiobdellid and though externally the bursa has the form found in genera with eversible penes, it is not clear that the penis of *Ankyrodrilus* is eversible (Holt, 1965, p. 16, fig. 9), while that of *Cronodrilus* is. In addition, species of *Ankyrodrilus* are flattened, not terete as in *Cronodrilus,* and the anterior nephridia open separately instead of by a common pore. The posterior segments of species of *Xironogiton* are flattened; the anterior nephridia open separately; the bursa, but not the penis, is eversible; the spermatheca is greatly reduced in size: in all of these respects *Xironogiton* differs from *Cronodrilus. Cirrodrilus* is an east Asian genus and includes all the species assigned by Yamaguchi (1934) to *Stephanodrilus.* The latter name is a junior synonym of *Cirrodrilus* (Holt, 1967b, p. 3). Both *Branchiobdella* and *Cirrodrilus* differ from *Cronodrilus* in having two anterior nephridiopores. The penis of *Cirrodrilus* is attached to the inner wall of the penial sheath (Yamaguchi, 1934, pp. 194–195), but that of *Cronodrilus* lies free in it. *Branchiobdella* has only one testicular segment (V) and both the penial sheath and spermiducal gland are excessively elongated, narrow tubes. *Cronodrilus* has two testicular segments. The penial sheath and spermiducal gland, while elongated and narrow, are not as excessively so as those of *Branchiobdella.* All these genera are related in various ways, particularly in the nature of the spermiducal gland and the absence of any

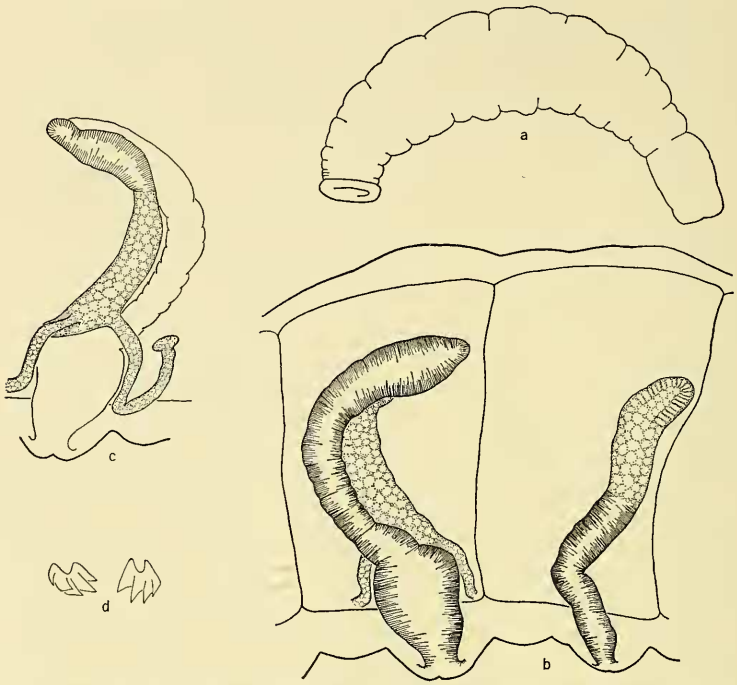

FIGURE 7. *Cronodrilus ogygius: a,* holotype; *b,* lateral view of reproductive systems; *c,* lateral view of male system viewed from side opposite that shown in 7b to show ejaculatory duct; *d,* oblique view of jaws, upper to the left.

type of prostate. Except for the common outlet of the anterior nephridia and the unbranched spermatheca, presumably advanced characters, *Cronodrilus* has the characteristics one would expect to find in the common ancestral stock of the genera with which it is compared.

Cronodrilus ogygius new species
Figures 7, 8

Type-specimens: Holotype and three paratypes, USNM 37103, three paratypes, PCH 1346, from *Cambarus latimanus* (LeConte), taken in a small stream, 3.1 miles north of Buchanan, Haralson County, Georgia, on U. S. Highway 27, by Perry C. and Virgie F. Holt, 25 March 1961.

Diagnosis: As for genus.

Etymology: From Greek, *ogygios,* of or pertaining to *Ogyges,* legendary king of Thebes, hence, primeval or ancient.

Description: Cronodrilus ogygius is a medium-sized worm of relatively slender proportions. Four animals of the type series (USNM 37104)

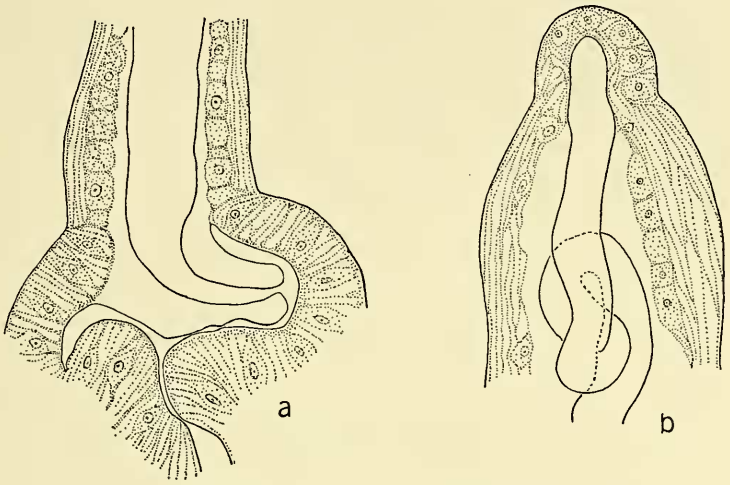

FIGURE 8. *Cronodrilus ogygius: a,* longitudinal optical section of bursal atrium and ectal end of penis; *b,* longitudinal optical section of junction of ejaculatory duct and penial sheath, and ental end of penis.

have the following dimensions: *total length,* 2.7–3.3 mm; *greatest diameter* (either segment VI or VII), 0.39–0.56 mm; *head length,* 0.45–0.49 mm; *head diameter,* 0.25–0.31 mm; *diameter, segment 1,* 0.26–0.31 mm; *diameter, sucker,* 0.29–0.30 mm.

The head is of usual proportions. The lips are entire, but the margin of the lower is slightly concave. There are no oral papillae. The external furrow encircling the head is shallow. There is only one pharyngeal sulcus. There are no supernumerary muscles in the prosomites of body segments and, consequently, the body outline is smooth (Fig. 7a). The clitellar glands of segment VI and VII are not prominent. The nephridiopore is on the dorsum of segment III.

The jaws are of usual size and the dental formula is 5/4, but the teeth are unusually large in proportion to the size of the jaws, sharply pointed, and subequal in length; the median ones slightly the longer. They are separated by deep grooves in the body of the jaws that extend almost to its base (Fig. 7d).

The vasa deferentia enter the spermiducal gland about ¼ of the total length of the latter from its ental end (Fig. 7c). The spermiducal gland is long and slender, about ⅕ of its length in diameter. There is no prostate or prostatic protuberance.

The ejaculatory duct is prominent (Fig. 7c), subequal to the spermiducal gland in diameter, about ½ its length, and set off by a slight constriction at its junction with the penial sheath of the bursa.

The bursa is distinctive. The penial sheath region is long, about ¾ the diameter of the body in length, and very slender (Fig. 7b). The wall of the penial sheath is composed of an outer longitudinal and an inner circular layer, both presumably muscular. The cuticular lining forms the eversible penis which lies free of the wall of the penial sheath, at least at its ental and ectal ends, except for the attachments to the atrium and ejaculatory duct (Fig. 8a, b), but along its midlength the wall of the penis and that of the penial sheath are so close to each other that their separateness cannot be determined. It is assumed, on the basis of the structure of the penis and penial sheath, that the penis is free, except at the ental and ectal ends, of its sheath and everts freely to form a double-walled cuticular tube. The atrium and its outlet canal make up about ¼ of the total length of the bursa. It is not certain that the usual inner atrial fold is present and the atrium is almost surely noneversible.

The spermatheca (Fig. 7b) has a long spermathecal duct. The bulb is of hardly greater diameter than the duct, but of the usual construction. An ental process is only slightly set off by a shallow constriction from the bulb and has a thick wall and narrow lumen. The exterior surface of the ental process appears wrinkled in the holotype.

Variation: The only observable variation is in the spermatheca. It is possible that the ental process is not a constant feature, but, rather is only present when the spermathecal bulb is incompletely filled with spermatozoa. Such processes do, however, seem to be constant features in some species, but an ental process of the spermatheca is not detectable in some of the specimens of the type series. Nonetheless, the congruence in other characters among these specimens is such that there can be no reasonable doubt as to their conspecificity.

Affinities: Since, at this time, *Cronodrilus* is a monotypic genus, the affinities of *C. ogygius* are those of the genus as discussed above.

Host: Cambarus latimanus (LeConte).

Distribution: Known only from the type locality.

Material Examined: The type specimens listed above.

Remarks: It is noteworthy that one collection from the Piedmont of Georgia should yield two such unusual branchiobdellids as *Sathodrilus megadenus* and *C. ogygius*. Though it is to be expected that both species will be found in other localities, it is likely that both are localized and rare.

Tettodrilus new genus

Type-species: Tettodrilus friaufi new species, here designated.

Diagnosis: Branchiobdellid worms with two pairs of testes; unpaired nephridiopore on dorsum of segment III; body terete, without peristomial tentacles, or dorsal projections on body segments; spermiducal gland slender, vasa deferentia enter entally; prostate non-differentiated, with bulb, incompletely divided from spermiducal gland; bursa ovoid to pyriform, penial sheath not externally demarkated from bursal atrium;

short eversible penis enclosed by muscular tube projecting into atrial lumen; ejaculatory duct present; spermatheca short, without ental process.

Etymology: From Greek, *tetta,* little father or daddy, and *drilus,* worm, in reference to the phylogenetic significance of the genus. Masculine.

Affinities: Tettodrilus is a primitive relative of the genus *Cambarincola* and its specialized descendants, the species of the genus *Pterodrilus. Pterodrilus* has been accorded monographic treatment (Holt, 1968b) and its relationships with *Cambarincola* discussed. Herein it is only necessary to compare *Tettodrilus* and *Cambarincola* and refer to the still more primitive *Sathodrilus,* to the aberrant *Ellisodrilus,* and *Oedipodrilus.*

The distinctive features of *Sathodrilus* in this context are the small and primitive spermiducal gland, the ental entry of the vasa deferentia into the gland, the rudimentary prostatic protuberance in some species, and the eversible penis. The spermiducal gland of *Tettodrilus* is slender with prominent deferent lobes at its ental end, obviously a tube formed by the union of the vasa deferentia, the epithelial wall of which has become glandular and rather like that, except for the relatively lesser diameter, of *S. carolinensis.* The prostatic protuberance of such species as *S. carolinensis* has become a true prostate, but one that is still incompletely divided from the spermiducal gland; that is, it does not empty into the ejaculatory duct at the place where the latter arises from the gland, but into the lumen of the spermiducal gland some distance entally to the ectal end of the gland. The prostate is slender, undifferentiated, but there is a prostatic bulb at its ental end that seems to be comparable to the prostatic protuberance in species of *Sathodrilus.* The penes of both *Sathodrilus* and *Tettodrilus* are eversible, but the two differ. The penis of *Tettodrilus,* unlike that of *Sathodrilus,* is enclosed in a very short penial sheath which is not separated from the bursal atrium by an external constriction. The eversible cuticular lining, that is the penis itself, is enclosed in a cylindrical, projecting (into the bursal atrium) tube that may be homologous with the inner atrial fold of other genera (see above, p. 302), but, more likely, is the evolutionary precursor of the protrusible penis (Fig. 9b). The jaws are similar, though those of *Tettodrilus* are more acutely triangular.

Tettodrilus resembles *Ellisodrilus* in the undivided and undifferentiated prostate, but otherwise, in the absence of a spermatheca and presence of a muscular, protrusible penis in *Ellisodrilus,* these genera are not alike. *Oedipodrilus,* likewise, has the same type of prostate, but the long, eversible penis of the latter is quite different from that of *Tettodrilus.*

The external (to the organs themselves) shape and arrangement of the components of the reproductive systems of *Tettodrilus* and *Cambarincola* are remarkably similar. They differ in the following ways: the spermiducal gland of *Tettodrilus* is a less compact, slenderer tube than in any known species of *Cambarincola;* the prostate is incompletely

divided from the spermiducal gland in *Tettodrilus*, but in species of *Cambarincola* it empties in common with the spermiducal gland into the ejaculatory duct; the bursa of *Tettodrilus* has the shape of that of *Cambarincola* and the ejaculatory ducts of the two are alike, but the penis of *Tettodrilus* retains its eversible character in contrast to the protrusible, cone-shaped, muscular penis of *Cambarincola* (Holt, 1949, p. 554). The jaws of the only known species of *Tettodrilus* and those of many species of *Cambarincola* are essentially identical; and the 5/4 dental formula of *T. friaufi* is most likely the primitive dental formula in the genus *Cambarincola*. *Tettodrilus*, in short, has the features expected in a primitive stock ancestral to the dominant genus *Cambarincola* and its specialized derivatives, but deserves, however, generic status on the basis of its primitive spermiducal gland and prostate and unusual eversible penis.

Tettodrilus friaufi new species
Figure 9

Type-specimens: Holotype, USNM 37099, and one paratype, USNM 37100, from *Orconectes rusticus mirus* (Ortmann), *O. rhoadesi* Hobbs, *Cambarus striatus* Hay, and *C. tenebrosus* Hay,[2] taken about 8.5 miles south of Lewisburg, Marshall County, Tennessee, in a small stream, on U. S. Highway 431, by Perry C. and Virgie F. Holt, 18 April 1960; one paratype, PCH 1007, from *Cambarus striatus* Hay and *C. tenebrosus* Hay, taken in a stream tributary to the Harpeth River, 2.4 miles south of Franklin, Williamson County, Tennessee on U. S. Highway 431, by Perry C. and Virgie F. Holt, 18 April 1960; one paratype, PCH 1008, from *Cambarus striatus* Hay, taken in a small stream, 5.3 miles south of Franklin, Williamson County, Tennessee, on U. S. 431, by Perry C. and Virgie F. Holt, 18 April 1960.

Diagnosis: As for genus.

Etymology: I am pleased to name this species for my friend, Dr. James J. Friauf, Jr., who collected the first recognized specimens of it.

Description: Tettodrilus friaufi is a medium-sized worm of graceful proportions. The specimens of the type series have the following dimensions: *total length*, 2.2–2.7 mm; *greatest diameter* (segment VI), 0.40–0.48 mm; *head length*, 0.41–0.49 mm; *head diameter*, 0.26–0.29 mm; *diameter, segment 1*, 0.27–0.33 mm; *diameter, sucker*, 0.26–0.29 mm.

The upper lip bears four lobes. Oral papillae are present, 10–12 in the holotype (they are difficult to count with certainty). There is only one encircling furrow of the head other than that which bounds the peristomium and it is very shallow. There is one pharyngeal sulcus. Segments II and III have weak supernumerary muscles, but the dorsal ridges of these segments are not prominent and the body outline is smooth. The clitellum is detectable, but not prominent, on the dorsa

[2] These specimens came from the sediments taken from the jar in which specimens of all four species of crayfish were collected.

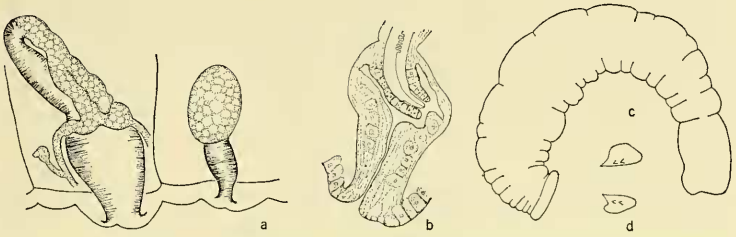

FIGURE 9. *Tettodrilus friaufi: a,* lateral view of reproductive systems; *b,* longitudinal optical section of bursa and penis; *c,* holotype; *d,* jaws, upper jaw above.

of segments VI and VII. The nephridiopore is usually easy to see on the dorsum of segment III.

The dental formula is 5/4. The median tooth of the upper jaw and the paramedian ones of the lower jaw are large and sharp. The upper jaw is noticeably larger than the lower. In color, both are a medium shade of brown.

The vasa deferentia are expanded and become glandular to produce deferent lobes of the spermiducal gland. The latter is about ½ the body diameter in length, slender, and frequently slightly bent so that it presents an irregular outline. It is subequal in diameter to the ejaculatory duct at the junction of the two.

The prostate appears in whole mounts to be histologically identical to the spermiducal gland, arises from the gland at about the border of the ectal and median thirds of the latter and extends entally to the junction of the deferent lobes. Its ental end contains a cavity, presumably equivalent to the prostatic bulb of many species of *Cambarincola* (Holt, 1949, p. 553; 1960, p. 63). In diameter, it is about ⅔ that of the spermiducal gland.

The ejaculatory duct is subequal in length and diameter to the spermiducal gland and an inner layer of circular muscle is prominent. It is set off from the penial sheath region of the bursa by a slight constriction.

The bursa is ovoid-pyriform. The ejaculatory duct passes almost directly into the atrium as a muscular tube about ⅓ as long as the bursa which encloses the eversible cuticular penis (Fig. 9b). This tube may be eversible, though it need not be for the penis to be everted. The outer end of the penis lies free within its enclosing tube and is a double-walled cylinder of cuticle that is transversely folded several times at the level of the junction of the ejaculatory duct and the bursa (Fig. 9b) so that it is capable of further eversion. But in the everted condition, it cannot be of any great length. The inner atrial fold is poorly developed and not at all prominent.

There is little to note concerning the spermatheca. The spermathecal duct is not unusually long, extending hardly farther than the ventral

border of the gut, and is of the usual structure, that is, there is no spermathecal bursa or other modifications of it. The bulb of the spermatheca is obovate. The muscle layer of the bulb is unusually thick and readily apparent at higher magnifications (400×) in whole mounts. There is no ental process.

Variation: There is no detectable variability, other than size, in the available material.

Affinities: The affinities of the genus *Tettodrilus* have been discussed above. Nothing further can be added: *T. friaufi* is not closely related to any known species of either *Sathodrilus* or *Cambarincola.*

Hosts: Cambarus striatus Hay, *C. tenebrosus* Hay, *Orconectes rhoadesi* Hobbs, and *O. rusticus mirus* (Ortmann). It is known from the field data that *T. friaufi* certainly occurs on both *C. striatus* and *C. tenebrosus,* but it is not certain that it occurs on the two species of *Orconectes* named.

Distribution: Streams of the Nashville Basin in Middle Tennessee. Other than localities mentioned above, *T. friaufi* has been taken from *Cambarus tenebrosus* in Percy Warner Park, near Nashville, Davidson County, Tennessee, by James J. Friauf, Jr., 22 March 1947.

Material Examined: In addition to the holotype and three paratypes, several poorly preserved specimens from Percy Warner Park, Davidson County, Tennessee, PCH 161, have been examined.

In anticipation of future discussions of the phylogeny of the branchiobdellids, the primitive nature and interesting distribution of the new genera and species described above deserve brief comment here. The species of *Sathodrilus,* particularly *S. carolinensis,* appear to be survivors of the stock that gave rise on one hand to *Ceratodrilus* and on the other to *Oedipodrilus.* By way of *S. veracruzicus, Sathodrilus* appears to be related to the relictual monotypic genus *Magmatodrilus* of northern California. *Cronodrilus* may well be a remnant of the stock that gave rise to all the branchiobdellids with the spermiducal glands that are produced entally beyond their junction with the vasa deferentia, including those of Asia and Europe except *Caridinophilia* Liang, 1963. *Tettodrilus* seems to be ideally suited to be an ancestor of *Cambarincola* and the latter's descendant genus *Pterodrilus.* As to their distribution: these putatively primitive forms occur in an arc around the southern end of the Appalachian Mountains and disjunctively in Mexico. It is tempting to theorize that those in the foothills of the Appalachians, remaining near their original homes, are relicts of ancient groups that gave rise to

the modern branchiobdellid fauna and that those in Mexico are remnants of likewise ancient stocks that somehow at an early time reached and have survived in the streams of the eastern flanks of the Sierra Madre Oriental.

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